Within-Plant and Temporal Distribution of Nymphal and Adult Western Flower Thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), on Flowers and Foliage of Greenhouse Impatiens, *Impatiens wallerana*, and Implications for Pest Population Sampling

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ABSTRACT The development of cost-effective management and sampling techniques for western flower thrips, *Frankliniella occidentalis* (Pergande), on garden impatiens, *Impatiens wallerana* (Hook. f.), requires that information about the within-plant distribution and diurnal patterns of thrips abundance be known. Impatiens flower bud development was divided into five arbitrary stages, representing tightly closed buds through fully opened flowers. Numbers of immature and adult thrips associated with these flower stages were determined at six times daily (0000, 0200, 0600, 0800, 1400, and 2000 hours). In addition, thrips distribution was determined among flowers with and without pollen, and on budless foliage, at two times daily (0800 and 0000 hours). Each successive stage of flower bud development contained significantly more adult female and immature thrips than the previous stage. The oldest flowers contained significantly fewer immature thrips than penultimate stage buds. There was no effect of sampling time on thrips density across flower bud stages. Flowers with pollen had significantly more adult female thrips compared with flowers without pollen, but numbers of adult male and immature thrips were not affected by presence of pollen. Foliage consistently contained the fewest of all life stages of thrips. There was a significant effect of time on female thrips abundance within the fully opened flower with pollen category and no effect of time on immature thrips abundance.

KEY WORDS *Frankliniella occidentalis*, western flower thrips, sampling, within-plant distribution

GARDEN IMPATIENS, *Impatiens wallerana*, is one of the most valuable bedding plant crops in the United States. The western flower thrips, *Frankliniella occidentalis*, is a major pest of impatiens, causing mechanical feeding damage and vectoring impatiens necrotic spot virus. As with any arthropod pest, knowledge of pest densities can be central to efficient pest management. To obtain this information, a reliable sampling plan for estimating thrips population density must be developed.

An initial step toward developing an efficient and practical sampling plan based on direct sampling of infested plants is determining an appropriate sample unit. The within-plant distribution of the western flower thrips has been determined for several crops including cotton (Pickett et al. 1988), roses (Linnamaki et al. 1998), greenhouse sweet peppers (Shipp and Zariffa 1991), greenhouse cucumbers (Steiner 1990), outdoor cucumbers (Rosenheim et al. 1990), and apples (Terry and DeGrandi-Hoffman 1988). Sampling flowers, which are often attractive to thrips (Gonzalez et al. 1982, Gonzalez and Wilson 1982, Pickett et al. 1988), is a common method of predicting both thrips presence and density, and has been used in apples (Terry and DeGrandi-Hoffman 1988), cucumber (Rosenheim et al. 1990, Wang and Shipp 2001) cyclamen (Williams 2001), and roses (Henneberry et al. 1964). Thrips abundance has been shown to fluctuate within flowers diurnally (Appanah and Chan 1981, Gonzalez and Wilson 1982, Kirk 1985, Tappan 1986, Pickett et al. 1988, Atakan et al. 1996, Atakan and Ozgur 2001, Kiers et al. 2000). Also, it has been shown on 'Granny Smith' apples that blossom cluster age (pink versus open versus petalless) affects thrips abundance (Terry and DeGrandi-Hoffman 1988). However, little is known regarding sampling of impatiens flowers to estimate thrips densities or if thrips exhibit diurnal patterns of abundance.

Knowledge of the within-plant distribution of thrips on impatiens plants is needed to identify sample units that will provide accurate estimates of thrips density. This study investigates how age and pollen status of impatiens flowers (i.e., with pollen or without pollen) affects thrips abundance. Pollens are known to increase both thrips fecundity and longevity (Trichillo and Leigh 1988, Lesky et al. 1997, Hulshof et al. 2003).

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We evaluated the fluctuation of thrips density at different times during the day. Depending on levels of diurnal movements, samples taken without regard to time of day might introduce excessive variation and bias to an estimate of thrips density. Information on thrips distribution in time and space will aid in designing better sampling protocols to detect treatment effects in research experiments; this will in turn help to generate a sampling protocol that can be used by growers. Additionally, knowledge of thrips distribution on impatiens could help to improve targeting and timing of pesticide applications. In this study, the abundance of immature and adult thrips was measured on impatiens foliage and flowers, collected at different times of day, to characterize the spatial and temporal distribution of the pest population on the host plant.

Materials and Methods

Plant Material

Cuttings of *Impatiens wallerana* variety 'SuperElfin; white', were taken from stock plants in November 2001 at Cornell University, allowed to root for 3–4 wk on a greenhouse misting bench, and potted with Pro-Mix BX (Premier Horticulture, Red Hill, PA) into 10.2-cm-diameter pots, with one plant per pot. Three adjacent greenhouses, each with ≈9 m^2 of bench space, were filled with 350–400 potted impatiens plants. Plants were grown under supplemental lighting 12:12-h light:dark, at 24 ± 6°C for 1 mo, which was sufficient for the plants to flower and for natural populations of western flower thrips to become established. Subsequent readings of impatiens flower samples revealed no other species of thrips present in the crop. Supplemental lighting was discontinued 1–2 d before the start of each experiment to allow thrips populations to adjust to the natural light regime (9:15-h light:dark). This allowed thrips to respond to the natural gradient of dawn to dusk as opposed to the abrupt light and darkness as occurs under supplemental lighting. Because most greenhouse growers in the northeastern United States do not use supplemental lighting, we felt that determination of diurnal patterns using this light regimen was justified. These plants were used in experiments 1, 2, and 4.

Impatiens plants, variety 'SuperElfin; white', used in experiment 3, were purchased as plugs (small rooted plantlets grown from seed) through a commercial plug producer (Cal Seedling Co., Arroyo Grande, CA). Individual plugs were potted in Pro-Mix BX, into 10.2-cm-diameter pots. Plants were grown in a greenhouse under the natural light regimen at 24 ± 3°C for 12 wk. Plants were trimmed once after 7 wk of growth and allowed to reflower before use (5 wk later).

Sampling Protocol

Flowers and foliage in all tests were removed from plants and immediately placed individually into 20-ml scintillation vials or 100-ml snap-cap polycarbonate vials containing 75% EtOH. Flower and foliage samples were dissected under alcohol in a glass petri dish using a stereomicroscope, and the numbers of immature, adult male, and female thrips were recorded for each sample. Thrips that were obviously dead before being placed into alcohol (i.e., dry and shriveled in appearance) were rare and were not quantified.

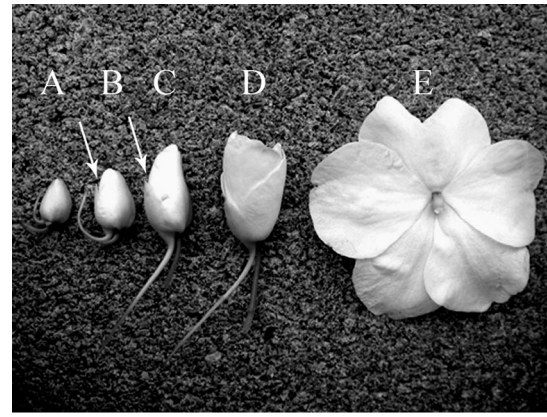

Fig. 1. Five stages of garden impatiens flower bud development sampled to determine thrips abundance within impatiens flowers. Flower bud stages: (A) unopened sepal, (B) split sepal, (C) split sepal, closed but expanding, (D) split sepal, petals unfurling, and (E) fully opened, nonsenescent flower. White arrows indicate the split between the sepal and flower petals by which thrips enter the developing flower bud.

Experiment 1: Effect of Flower Developmental Stage and Time of Day on Thrips Abundance. To determine the distribution of western flower thrips among flowers of various developmental stages, the development of impatiens flowers was arbitrarily divided into five stages: A, B, C, D, and E (Fig. 1). These flower stages matured to the subsequent flower stage in ≈4, 2, 1, and 1 d, respectively. When the flower petals begin to expand, a small opening develops between the petals and the sepal. This provides an opening through which thrips can enter the developing bud. Stage A designated any flower bud whose sepal had yet to break away from the petals (no opening between the petals and sepals). Stage B designated any flower bud whose sepal had broken away from the bud by <2 mm. Stage C flower buds were those with sepal-bud openings between 3 and 5 mm and with petals still expanding. Petals of stage D flowers were in the process of unfurling, and stage E samples were fully opened nonsenescent flowers.

The five flower stages were sampled from each randomly selected plant in all three replicated greenhouses at six times of day (0800, 1400, 2000, 0000, 0200, and 0600 hours) on sample dates 24 and 31 January and 6 February 2002. Preliminary samples conducted at four times of day (0800, 1400, 2000, and 0000 hours) indicated a drop in thrips abundance some time between 0000 and 0800 hours. Thus, two additional sample times were added in an effort to more accurately determine when the drop in thrips abundance occurred. All times were chosen for their relative con-

venience. On the first sample date (24 January 2002), five replicate samples were taken from each greenhouse at four of the six times (0800, 1400, 2000, and 0000 hours). The number of samples/greenhouse/time was reduced to a more manageable three replicates for all subsequent samplings, yielding a total of $n = 11$ replicate samples at times 0800, 1400, 2000, and 0000 h and $n = 9$ samples at 0000 and 0200 hours (per greenhouse per sample time). The numbers of immature and adult thrips were tallied for the first sample date and the numbers of immature, adult male, and adult female thrips were tallied for the last four sample dates.

Experiment 2: Effect of Pollen on Thrips Abundance in Fully Opened (E-stage) Flowers and Comparison of Thrips Abundance in Flowers Versus Foliage at Two Sample Times. Closer inspection of stage E flowers revealed two distinctive types: those with and those without pollen. Adult thrips appeared to be most abundant on those stage E flowers that were shedding pollen (T.A.U., unpublished data). This led us to conduct replicated tests over time in a single greenhouse to determine if the presence of impatiens pollen influenced thrips abundance. Thrips were sampled in fully opened flowers with pollen, in fully opened flowers whose anthers had been artificially removed, and on foliage from plants with and without pollen-bearing flowers. Open flowers and flower buds were removed from the plants in one of the greenhouses used in experiment 1 for 3–5 d to reduce numbers of thrips in the system and maintain plant health. Forty plants were chosen randomly from among the 350 plants in the greenhouse. These 40 plants were flagged and randomly assigned to one of two treatments: with pollen or without pollen (20 plants per treatment). One stage D flower was randomly selected on each of 40 plants 24 h before initial sampling at 0800 hours. The anthers (pollen bearing structure) of stage D flowers in the no pollen treatment were emasculated by drawing a razor blade along the tissue (top to bottom) supporting the anthers to remove all pollen. Stage D flowers in the pollen treatment were not emasculated, leaving their pollen intact. All plant parts to be sampled had a small piece of red tape affixed to the flower pedicel for rapid location at the time of sampling. In addition, 10 plants, 5 from each treatment, were randomly chosen and designated to have one 5–6 cm length of terminal stem sampled for thrips. All flowers and flower buds were removed from these stems 24 h before sampling so that only thrips from the foliage would be recovered. After 24 h, the stage D flower buds had developed to stage E flowers. Ten flowers from each treatment and 10 terminal stem samples (5 from each of the two flower treatments) were removed at 0800 and 0000 hours. These times were chosen based on the results from experiment 1, which suggested they were near the peak and trough of thrips abundance patterns. The entire experiment was conducted on three sample dates: 19–21 February 2002. The numbers of immature, adult male, and adult female thrips in each sample were recorded.

A sham emasculation test was conducted to determine if handling flowers during emasculation could have led to dispersal of thrips. The pedicils of 32 stage D flower buds were tagged with red tape 24 h before sampling. One half were taken in hand, and a razor blade was brought down to the pollen-bearing structure and retracted. After 24 h, the stage D flower buds had developed to stage E flowers. The numbers of immature, adult male, and adult female thrips in each sample were recorded.

Experiment 3: Comparison of Thrips Abundance in Stage D Flower Buds, Stage E Flowers with Pollen, and Stage E Flowers Without Pollen. Observations of impatiens flowers revealed two types of fully opened (stage E) flowers, those with pollen and those whose androecium, which bears the stamens and thus pollen, had dropped (i.e., fallen from the plant). The pistol of an impatiens flower is covered by the androecium. As the pistol develops, it grows both upward and out, and the androecium splits at its base, dries out, and falls from the flower, revealing the pistol. Typically, the stamens on dropped androecia retain very little if any pollen. Similarly, the amount of pollen shed onto petals is negligible in comparison to that located on the stamens (T.A.U., unpublished data). To determine if thrips abundance was affected by the age and condition of the androecium (i.e., with and without pollen), an experiment was conducted to compare thrips abundance in stage D flower buds, which have pollen, and stage E flower buds with and without pollen (lost naturally). The hypothesis was that thrips abundance in stage E flowers with pollen would not be different from abundance in stage D flowers but would differ from abundance in stage E flowers whose androecium had been dropped (without pollen).

Samples of each of the three plant parts were removed from randomly selected plants. All flower samples were removed at the same time (1200 hours) on three different dates ($n = 20$ samples/sample unit/date; 24 and 29 September and 3 October 2003). Because we were not interested in the effect of time on thrips abundance in this study, the sampling time, 1200 hours, was chosen for its convenience. The numbers of immature, adult male, and adult female thrips in each sample were recorded.

Experiment 4: Effect of Time of Day on Thrips Abundance on Foliage in the Absence of Flower Buds. An experiment was conducted to determine if thrips exhibited diurnal shifts in abundance on impatiens foliage in the complete absence of both flower buds and opened flowers, such as during crop growth before the onset of flowering. For 1 wk before the start of the experiment and for the duration of the sample dates, all flowers and developing buds with split sepals were removed daily from every plant in the greenhouse to simulate the flowerless environment. Fifty plants were randomly chosen from 360 potted plants in one greenhouse on each of three sample dates (28 February and 4 and 5 March 2002). Ten plants from among the 50 were randomly selected to be sampled at each of five sample times (0800, 1400, 2000, 0000, and 0200 hours). One stem per plant was randomly

Table 1. Times of plant part collection, plant parts collected in observational and experimental studies, and experimental treatments where applicable

	Time of Day	Plant part
Experiment 1[a]	0000, 0200, 0600, 0800, 1400, and 2000 hours	Stage A, B, C, D, E flower buds and flowers (see Fig. 1)
Experiment 2[b]	0000 and 0800 hours	Stage E flowers with pollen
		Emasculated stage E flowers (treatment)
		Budless flowerless stems (treatment)
Experiment 3[c]	1200	Stage D flowers
		Stage E flowers with pollen
		Stage E flowers without pollen (lost naturally)
Experiment 4[d]	0800, 1400, 2000, 0000, and 0200 hours	Budless flowerless stems

[a] Observational sample units, flower stages A–E, collected from greenhouse grown garden impatiens infested western flower thrips at six times of day once a week for 3 wk.

[b] Experimental potential sample units were flowers with and without pollen (emasculated) and budless flowerless stems collected from greenhouse grown garden impatiens infested with the western flower thrips two times of day for 3 consecutive d.

[c] Observational potential sample units, stage D flowers and stage E flower with and without pollen (lost naturally), collected from greenhouse grown garden impatiens infested with the western flower thrips at 1200 hours. Samples were collected on three dates at 5-d intervals.

[d] Observational sample units, budless flowerless stems, collected five times a day from greenhouse grown garden impatiens infested with the western flower thrips on three sample dates within a 6-day period.

selected from each pot for sampling. The top 7 cm of a terminal end of budless stem was cut from each plant and placed into ethanol filled vials. The numbers of immature, adult male, and adult female thrips in each sample were recorded.

Statistical Analysis

Computations for all experiments were made using the statistical software package JMP version 4 (SAS Institute 2001). Data from all assays were transformed using $\log(x + 1)$ to normalize aggregated populations. All experiments were conducted on multiple dates to test the repeatability of the responses. This resulted in autocorrelation of the data among sample dates within each greenhouse. Thus, multivariate analysis of variance (MANOVA) was conducted on numbers of adult male, adult female, and total numbers of immature thrips from each experiment, treating date as a repeated measure. The statistical model in experiment 1 included the main effects of flower stage (five stages) and time of day (six times of day), as well as the blocking factors greenhouse (three blocks) and plant (three plants for four times on the first date, five plants thereafter). The interaction term between the two main effects and all two and three way interactions with the repeated measure variable date were also included. The statistical model in experiment 2 included the main effects of plant part (three plant parts) and time of day (two times), the interaction term between the two main effects, and all two and three way interactions with the repeated measure variable date. The statistical model in experiments 3 included the main effect of flower stage (three stages) and the interaction term between flower stage and the repeated measure variable date. The statistical model in experiments 4 included the main effect of time of day (five times) and the interaction term between time of day and the repeated measure variable date. For all statistical tests, insignificant interactions were reported and dropped from statistical models and analyses rerun; this leads to differences in the degrees of freedom error reported for test of interactions and main effects among life stages when interactions are insignificant. Mean separations, where applicable, were conducted using Tukey's honestly significant difference (HSD) test ($P < 0.05$). See Table 1 for a list of sample units and sample times for each experiment.

Results

Experiment 1

Effect of Flower Development Stage on Thrips Abundance. Experiment 1 was designed to determine thrips distribution on five different developmental stages of impatiens flower buds and whether thrips exhibited diurnal patterns of abundance. The stage of impatiens bud development had a highly significant effect on thrips abundance for all thrips life stages (females: $F_{(4,253)} = 79.0$, $P < 0.0001$; males: $F_{(4,253} = 21.6$, $P < 0.0001$; immatures: $F_{(4,253)} = 186.4$; $P < 0.0001$; Fig. 2). As buds matured from stages A to D, the mean number of adult female and immature thrips per flower increased 176 and 29 times, respectively. This increase was followed by a significant decrease, 0.74 times, in immature thrips abundance from stage D to stage E buds (Fig. 2). The range and the mean ± SE number of adult female and immature thrips, respectively, reached a peak density of 2.5–2.8 female thrips and 8.5 ± 0.5 immature thrips per stage D bud. The mean ± SE number of adult males increased from zero in stage A buds to a maximum of 0.4 ± 0.1 per stage E bud.

Effect of Time of Day on Thrips Abundance. There was no effect of time of day on thrips abundance for any life stage (females: $F_{(5,253)} = 1.3$, $P = 0.27$; males: $F_{(5,253)} = 1.8$, $P = 0.12$; immatures: $F_{(5,253)} = 1.8$, $P = 0.12$; Fig. 2). There was not a significant time of day × flower stage interaction for any thrips life stage (females: $F_{(20,233)} = 0.7$, $P = 0.81$; males: $F_{(20,233)} = 1.2$, $P = 0.29$; immatures: $F_{(20,233)} = 0.9$, $P = 0.55$; Fig. 2). There was a significant date × flower stage interaction for female and male thrips, and there were no other significant two-way or three way main effect × date interactions (Table 2). We suspected that our indis-

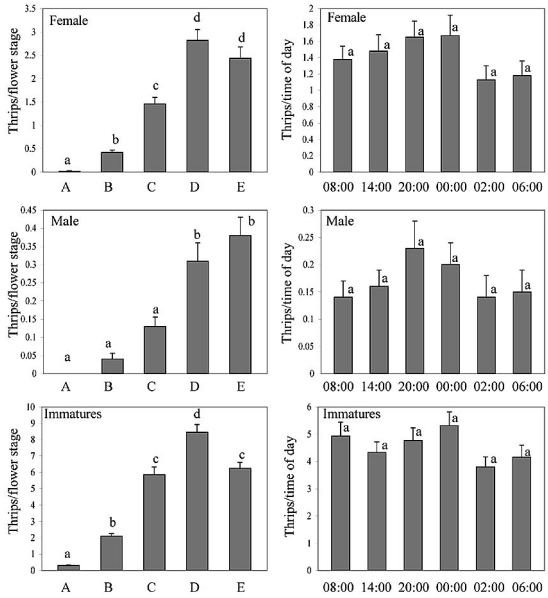

Fig. 2. Mean thrips per flower bud stage sampled at six times of day (0800, 1400, 2000, 0000, 0200, and 0600 hours) and mean thrips per time (pooled across flower stage). Means ± SE of a given life stage with the same letter above the bar are not significantly different (Tukey's HSD test; $\alpha = 0.05$).

criminant choice of stage E flowers with pollen versus stage E flowers without pollen was the cause for this interaction; different ratios of the two types of stage E flowers were selected among dates. When stage E flowers were excluded from the analysis for females, the date × flower stage interaction was not significant ($F_{(6,400)} = 0.5$, $P = 0.84$); similarly, when stage D and stage E flowers were left undifferentiated in the analysis, the interaction was no longer significant ($F_{(6,508)} = 0.4$, $P = 0.89$). We suspect that the significant date × flower stage interaction for males was an artifact of sampling the exceedingly low-density male population (0.17 ± 0.02).

Experiment 2

Effect of Pollen on Thrips Abundance in Fully Opened Flowers (stage E) and Comparison of Thrips'

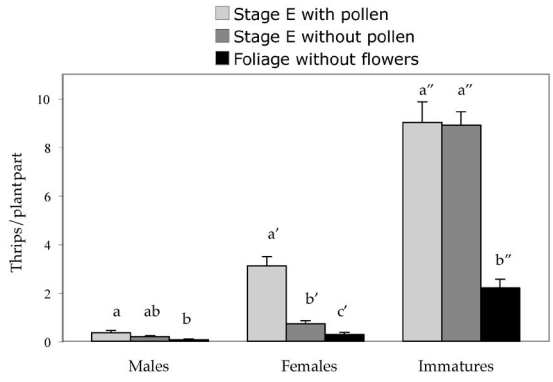

Fig. 3. Thrips per plant part (stage E flower with pollen, stage E flower without pollen, bud-less foliage) pooled across two sample times (0800 and 0000 hours). Means ± SE of a given life stage with the same letter above the bar are not significantly different (Tukey's HSD test; $\alpha = 0.05$).

Abundance in Flowers and Foliage. Thrips abundance differed significantly among stage E flowers with pollen, stage E flowers without pollen, and foliage without flowers and buds for all thrips life stages (females: $F_{(2,54)} = 64.5$, $P < 0.0001$; males: $F_{(2,56)} = 7.4$, $P = 0.001$; immatures: $F_{(2,56)} = 69.1$, $P < 0.0001$). Significantly fewer female and immature thrips occurred on foliage without flowers and buds compared with flowers with and without pollen; fewer males were found on foliage compared with flowers with pollen, and the number of males on flowers with pollen did not differ significantly compared with stage E flowers without pollen (Fig. 3). Numbers of immature thrips, which accounted for 81% of the total thrips quantified, did not differ between flowers with pollen versus flowers without pollen. Adult females, which account for 16% of all thrips quantified, were significantly more abundant in flowers with pollen compared with flowers without pollen. There was also no effect of sham-emasculation on thrips abundance (females: $F_{(1,29)} = 0.03$, $P = 0.49$; males: $F_{(1,29)} = 0.6$, $P = 0.46$; immatures: $F_{(1,29)} = 0.0004$, $P = 0.98$; data not shown). An additional test was conducted to test if thrips abundance differed among stems that had their flowers removed 24 h before sampling versus just before sampling. There was no statistical difference in the abundance of any thrips life stage (data not shown).

Table 2. ***F*-statistics and *P* values for block effects and the repeated measure variable date × treatment interactions for experiment 1**

Factor[a]	*F*-statistics		
	Females	Males	Immatures
Greenhouse (block)	$F_{(2,253)} = 14.6$, $P < 0.0001$	$F_{(2,253)} = 7.1$, $P = 0.001$	$F_{(2,253)} = 22.1$, $P < 0.0001$
Plant (block)	$F_{(2,253)} = 0.4$, $P = 0.68$	$F_{(2,253)} = 0.1$, $P = 0.89$	$F_{(2,253)} = 0.6$, $P = 0.57$
Date (repeated measure variable)	$F_{(2,252)} = 2.0$, $P = 0.14$	$F_{(2,252)} = 0.82$, $P = 0.44$	$F_{(2,252)} = 7.1$, $P = 0.001$
Date × time of day	$F_{(10,506)} = 1.1$, $P = 0.37$	$F_{(10,506)} = 1.1$, $P = 0.04$	$F_{(10,506)} = 1.2$, $P = 0.28$
Date × flower stage	$F_{(8,506)} = 2.1$, $P = 0.03$	$F_{(8,506)} = 2.8$, $P = 0.005$	$F_{(8,506)} = 1.5$, $P = 0.17$
Date × time of day × flower stage	$F_{(40,466)} = 1.1$, $P = 0.26$	$F_{(40,466)} = 0.7$, $P = 0.88$	$F_{(40,466)} = 0.9$, $P = 0.66$

[a] All potential sample units (five stages of impatiens bud development, Fig. 1) were collected from three randomly selected replicate plants in each of three replicate greenhouses on three dates.

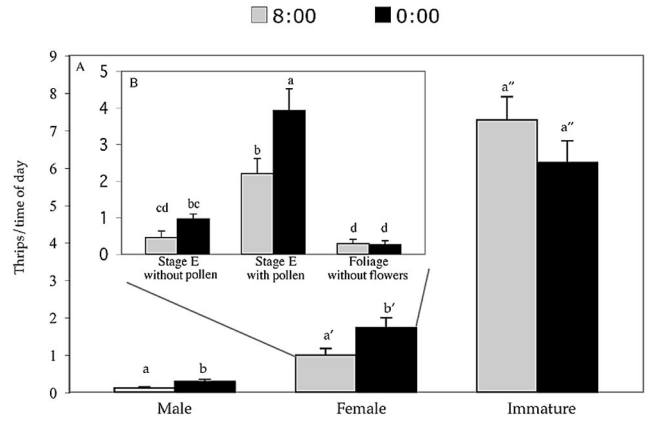

Fig. 4. (A) Thrips per sample time (0800 and 0000 hours) pooled across three potential sample units (stage E flower with pollen, stage E flower without pollen, budless foliage). (B) Adult female thrips per potential sample unit at the two sampling times; significant time of day by flower stage interaction. Means ± SE of a given life stage with the same letter and above the bar are not significantly different (Tukey's HSD test; $\alpha = 0.05$).

Effect of Time of Day on Thrips Abundance. Across the three plant parts described in the preceding section, samples taken at 0000 hours had significantly more adult females and males (1.7 and 2.5 times more, respectively) than samples that were taken at 0800 hours (females: $F_{(1,54)} = 12.4, P = 0.0009$; males: $F_{(1,56)} = 7.3, P = 0.009$; Fig. 4A). There was not a significant main effect of time of day on immature thrips abundance ($F_{(1,56)} = 2.3, P = 0.14$). Additionally, there was not a significant time of day × plant part interaction for male or immature thrips (males: $F_{(2,54)} = 1.2, P = 0.32$; immatures: $F_{(2,54)} = 1.3, P = 0.27$); however, there was for female thrips ($F_{(2,54)} = 4.0, P = 0.02$). The interaction arises from the fact that female thrips abundance on stage E flowers with pollen was significantly different at the two times sampled, whereas there was not a significant difference in thrips abundance on the remaining two plant parts among the two times tested (Fig. 4B). There was also no time of day by date interaction for any thrips life stage (females: $F_{(2,53)} = 1.8, P = 0.18$; males: $F_{(2,55)} = 2.4, P = 0.10$; immatures: $F_{(2,55)} = 0.7, P = 0.49$), or a date × plant part interaction (females: $F_{(4,108)} = 1.9, P = 0.11$; males: $F_{(4,110)} = 0.9, P = 0.48$; immatures: $F_{(4,110)} = 1.5, P = 0.21$). The significant time of day × treatment interaction for female thrips did not depend on the repeated measure date ($F_{(4,108)} = 1.3, P = 0.26$).

Experiment 3: Comparison of Thrips Abundance in Stage D Flower Buds, Stage E Flowers with Pollen, and Stage E Flowers Without Pollen

A study was undertaken to determine if the presence of pollen with respect to flower age (old flowers do not have pollen) had an effect on thrips abundance. The abundance of adult female and immature thrips varied significantly among the potential sample units (females: $F_{(2,57)} = 109.7, P < 0.0001$; immatures: $F_{(2,57)} = 23.5, P < 0.0001$), but adult male abundance did not ($F_{(2,57)} = 1.5, P = 0.24$; Fig. 5). The greatest numbers of female and immature thrips among the three flower stages (58 and 44% of each respective population) were found on stage E flowers with pollen.

Experiment 4: Effect of Time of Day on Thrips Abundance on Foliage in the Absence of Flower Buds

The numbers of all thrips life stages collected from stems of flowerless impatiens plants with the buds removed did not differ significantly by time of day (female: $F_{(4,43)} = 0.4, P = 0.81$; male: $F_{(4,43)} = 2.1, P = 0.10$; immatures: $F_{(4,43)} = 1.5, P = 0.22$) but did differ significantly by date (female: $F_{(2,42)} = 23.3, P < 0.0001$; male: $F_{(2,42)} = 29.1, P < 0.0001$; immatures: $F_{(2,42)} = 4.4, P = 0.02$; Fig. 6). Additionally, there was not a significant date by time of day interaction for any thrips life stage (female: $F_{(8,86)} = 0.5, P = 0.82$; male: $F_{(8,86)} = 1.3, P = 0.25$; immatures: $F_{(8,86)} = 1.1, P = 0.38$).

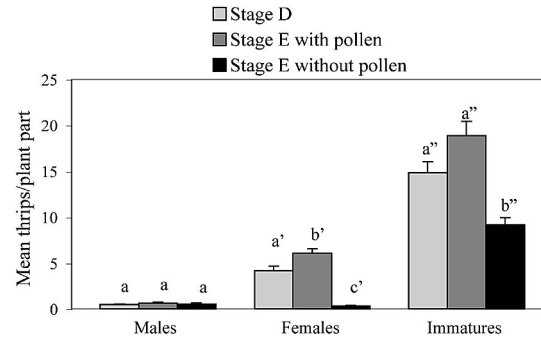

Fig. 5. Thrips per flower bud stage (stage D, stage E with pollen, stage E with pollen lost naturally). Means ± SE of a given life stage with the same letter above the bar are not significantly different (Tukey's HSD test; $\alpha = 0.05$).

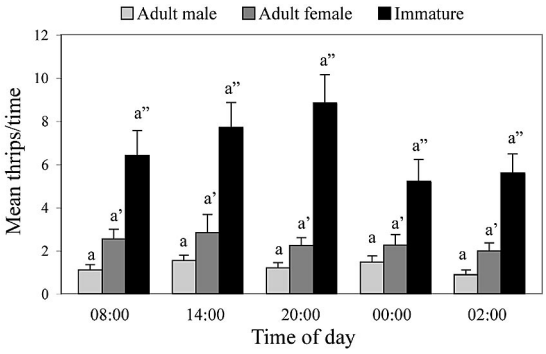

Fig. 6. Mean thrips at five times of day, sampled from budless and flowerless impatiens foliage. Means ± SE of a given life stage with the same letter above the bar are not significantly different (Tukey's HSD test; $\alpha = 0.05$).

Discussion

Experiment 1 revealed that once the bud sepals split from the petals (stage B), all stages of thrips (male and female adults and immatures) were detected in and on the buds (Fig. 2). The abundance of all stages of thrips increased as the buds developed to the stage when buds began to unfurl (stage D). The subsequent decrease in the number of thrips from stage D buds to stage E (fully opened) flowers, which was a significant drop for immature thrips but not for females, was unexpected and was most likely caused by inadvertent, indiscriminate sampling of nonsenescent fully opened flowers. Two types of flowers were present, those with pollen and those without their androecium (and thus without pollen), which drops off as the pistol matures (3–5 d after fully opening). The greatest number of female thrips appeared to be on fully opened flowers that still retained their pollen.

Experiment 2 tested the hypothesis that thrips preferred flowers with pollen by artificially removing pollen from selected flowers. Adult females were more abundant in flowers with pollen compared with pollenless flowers. There were 2.5 times more males on flowers with pollen compared with flowers without pollen, although a statistically significant difference was not detected. Immature thrips abundance, however, did not differ among flower types. It has been shown in studies of other plant species that thrips abundance declines with flower age (Kirk 1985, Tappan 1986, Atakan and Ozgur 2001). In this experiment, flower age was controlled by artificially removing pollen from young flowers, and the lack of a difference in immature abundance between the two flower types is, therefore, not surprising. The results from experiment 2 support our hypothesis that the decrease in female and immature thrips abundance from stage D to stage E flowers observed in experiment 1 was caused in part by the inadvertent inclusion of pollenless stage E flowers among the stage E flower samples. Counts of all open flowers on a random sample of plants (similar in age to those used in experiment 1) revealed that ≈75% of open flowers were pollenless (data not shown).

Further exploration of the hypotheses (1) that the decline in thrips abundance from stage D flower buds to stage E flowers in experiment 1 was caused by the inadvertent inclusion of pollenless stage E flowers and (2) that stage E flower age affects immature thrips abundance was carried out in experiment 3 by sampling stage D buds and the two types of stage E flowers, without controlling for age of stage E flower. Our initial hypothesis was confirmed; most female thrips were found on stage E flowers with pollen (confirming results in experiment 2), followed by stage D buds, and finally stage E flowers without pollen. The increase in the abundance of female thrips from stage D to stage E flowers is most likely a result of recruitment. Pollen begins to mature in stage D flowers, and adult female thrips may migrate in increasing numbers to these flowers. Immature thrips abundance among the three flower stages followed the same trend as adult females; there were significantly more immature thrips on young stage E flowers (with pollen) compared with the older stage E flowers (without pollen), and immature thrips abundance in stage D flowers was intermediate, although not statistically different from flowers without pollen. Adult female thrips feeding on pollen likely deposit eggs in the flower tissue of stage D and young stage E flowers. Thrips eggs hatch in ≈2 d at 25°C, which is approximately when stage D flowers mature to stage E flowers, thus accounting for the increase in the immature population from stage D to stage E flowers. It is also possible that immature thrips detect flower senescence or pollen presence/absence and migrate to younger flowers, preferring flowers with pollen; although results from experiment 2 indicated that immature thrips do not show a preference for flowers with pollen versus those without when age of flower is controlled for.

Time of day did not have a significant effect on abundance of any thrips life stage in experiment 1, whereas time of day significantly affected abundance of female and male thrips in experiment 2. Numbers of all life stages of thrips generally climbed steadily throughout the day, peaked between 2000 and 0000 hours, and were lowest between 0200 and 0600 hours (Fig. 2). The results from experiment 2 were similar to this pattern in that, on all three sample dates, both adult males and females were found in greater numbers at 0000 compared with 0800 hours (Fig. 4). Regardless of statistical significance, the effect of time on thrips abundance was never great (range of differences between the highs and lows of 0.09–1.5 thrips) and would likely not contribute to a large bias in flower samples used to estimate thrips densities in crops of garden impatiens for experimental purposes, especially when all treatments will likely be sampled at the same time.

These results are in sharp contrast to the findings of other researchers studying the effect of time on abundance of thrips in flowers. Kirk (1985) found that numbers of *Thrips major* Uzel and *Thrips fuscipennis* Haliday, in flowers of hedge weed, began building after dawn and declined after 1200 hours. Atakan and Ozgur (2001) sampled young (white) cotton flowers

and old (red) cotton flowers for *Frankliniella intonsa* (Trybom) over time. In white flowers, numbers increased and peaked ≈1200 hours, and in red flowers, numbers decreased and reached the lowest density at 1200 hours. The authors suggested that this is strong evidence that thrips leave old (red) flowers and migrate to young (white) flowers. Kiers et al. (2000) and Tappan (1986) found that *F. occidentalis* and *Frankliniella fusca* (Hinds) reached peak abundance in crops of peanut and greenhouse cucumber at 1200 hours and decreased thereafter. In each of these instances, the flowers being sampled are typically opened for only 24 h, with the exception of cotton, which may remain open for up to 48 h before wilting. In contrast, impatiens flowers may remain open for up to 7 d before showing signs of wilt, and they may produce pollen for 2–3 d, giving females thrips an extended opportunity to feed on pollen compared with short-lived flowers. This may explain why there is no marked peak in thrips abundance in impatiens at midday.

Experiments 2 and 4 revealed that there was no effect of time of day on thrips abundance on foliage samples taken in the presence or absence of flowers. There was an apparent peak in immature abundance on foliage at 2000 hours (Fig. 6), which corresponds to the temporal pattern of thrips abundance on flowers seen in experiment 1. Given that the diurnal pattern in thrips abundance is evident in both the flowerless and flowering environments suggests that temporal shifts in thrips abundance are not a function of the presence of flowers or the resources associated with flowers, like pollen. The mechanism behind these weak temporal shifts in thrips abundance is unclear, and in the context of developing a sampling plan or improving targeting or timing of insecticidal spray applications, the time factor would seem relatively unimportant. An explanation as to the shifts in thrips abundance is unclear and may warrant further study.

Gerin et al. (1999) determined that the abundance of female western flower thrips varied between foliage and flowers of impatiens plants and showed that flowers were essential for rapid western flower thrips population growth. They hypothesized that flowers might serve as mating sites as shown by Rosenheim et al. (1990) or that flowers may somehow provide "special nutrients" that are essential for thrips development. They provide support for each of the two hypotheses and suggest that a lack of flowers could affect survival and fecundity, and go on to cite examples of pollens improving demographical patterns of thrips. Experiments 1–3 revealed that adult female thrips exhibit a strong preference not only for flowers over foliage, but more specifically for flowers with pollen, as shown explicitly in experiment 2 (Fig. 3). Gonzalez et al. (1982), Gonzalez and Wilson (1982), and Pickett et al. (1988) have shown that *F. occidentalis* abundance is greatest in cotton flowers compared with foliage. Similarly, Rosenheim et al. (1990) showed that *F. occidentalis* was more commonly found in flowers of monoecious cucumber plants compared with leaves, and cites Bryan and Smith (1956), Yudin et al. (1986), Pickett et al. (1988), and Yudin et al. (1988) as having noted flowers' attractiveness to *F. occidentalis.* In addition, the positive effects of pollen on thrips longevity and fecundity have been shown numerous times (Murai and Ishii 1982, Kirk 1984, 1985, Trichillo and Leigh 1988, Lesky et al. 1997, Hulshof et al. 2003), and this likely accounts for thrips' preference for flowers with pollen. In light of the results reported herein, the ability of pollens to act as a thrips attractant and arrestant seems the logical explanation for much of the attractiveness of flowers to thrips reported in the literature; however, few studies have investigated specifically the role of pollen in thrips attraction to flowers (Atakan and Ozgur 2001, Gerin et al. 1999). Given that thrips fecundity and longevity increase when pollen is available, manipulating the abundance of this resource could have widespread implications for managing thrips populations.

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